SYSTEMATIC RELATIONSHIPS AND ZOOGEOGRAPHY OF THE WHITE-WINGED GUAN (*PENELOPE ALBIPENNIS*) AND RELATED FORMS

J. WILLIAM ELEY

The avian genus *Penelope* (Cracidae), comprising 13–15 species (depending on the authority), is widely distributed from northeastern Mexico south to Argentina and Uruguay. Relationships within this genus are obscure, as reflected by the variation in recent taxonomic treatments (Vuilleumier 1965, Vaurie 1968, Delacour and Amadon 1973). There is general agreement by these authors that members of the genus fall into several species groups, although the exact composition and arrangement of these groups are also debated. Vuilleumier (1965) divided the genus into four species groups, and included species of *Pipile* in *Penelope*. Vuilleumier's (1965) conclusion that there are only eight species of *Penelope* (including *Pipile*) was not accepted in two subsequent treatments of the family. Vaurie (1968) and Delacour and Amadon (1973) generally agreed that the genus is divisible into one group of small species (*P. montagnii* [Andean Guan], *P. argyrotis* [Band-tailed Guan], *P. barbata* [Bearded Guan], *P. marail* [Marail Guan], *P. ortoni* [Baudó Guan], and *P. superciliaris* [Rusty-margined Guan], and two groups of large-sized species (*P. purpurascens* [Crested Guan], *P. jacquacu* [Spix's Guan], *P. obscura* [Dusky-legged Guan], *P. dabbenei* [Red-faced Guan], and *P. albipennis* [White-winged Guan] forming one group; and *P. pileata* [White-crested Guan], *P. ochrogaster* [Chestnut-bellied Guan], and *P. jacucaca* [White-browed Guan] the second).

Although all authorities have agreed that *P. albipennis* is most closely related to the *P. purpurascens-jacquacu* complex, there has been little speculation on its phylogenetic history. *P. albipennis* was thought to be extinct until its rediscovery in 1977, and the lack of a sufficient number of specimens and natural history information on the species made spec-

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ulations on its affinities extremely tenuous. New information available on *P. albipennis*, including its vocalizations, has facilitated a systematic study of this species and its closest congeners. In this paper I examine the relationships within several of the large species of *Penelope* and present a model for the speciation of these forms during the Pleistocene.

P. dabbenei was not included in this study due to the scarcity of specimens and information on its natural history. It is considered by most workers to be an isolated subtropical zone relative of *P. obscura*.

DISCOVERY, DISTRIBUTION AND CURRENT STATUS OF *P. ALBIPENNIS*

P. albipennis was described in 1877 by Taczanowski from a specimen collected by Stolzmann in mangroves near the mouth of the Río Tumbes in northwestern Peru (Taczanowski 1877). A second specimen, a female, was taken a month later by Jelski at the Hacienda de Pabur near the town of Piura. This female was accompanied by two chicks, one of which was captured alive and raised, and became the third known specimen of *P. albipennis* (Vaurie 1966a). The species was considered rare by Stolzmann (Ogilvie-Grant 1896), and despite attempts by Maria Koepcke to find the bird in the 1950's and 1960's and by Gustavo del Solar in the 1970's, it was not seen or collected again until September 1977, when a small population was found by del Solar and John P. O'Neill at San Isidro, northeast of Olmos, near the Lambayeque-Piura border. O'Neill and del Solar were alerted to the presence of the species when a local farmer produced two birds which he had shot near his farm. Subsequent work has shown that the currently known range of *P. albipennis* lies entirely in the Dept. Lambayeque, from east of Ñaupe south to near Chongoyape, east of Chiclayo (Enrique Ortiz T., pers. comm.). In the past it probably extended from the Ecuadorian border south to the Río Chicaina [=Chicama?] in La Libertad (a range that coincides with the previous extent of suitable habitat) (Delacour and Amadon 1973). The species inhabits the dry wooded slopes and ravines of the western foothills of the Andes from ca. 300–500 m elev. (see Williams 1980). Because the first specimens were taken at the mouth of the Río Tumbes, *P. albipennis* may well have occurred in coastal gallery forests; its restriction to the Andean foothills is probably due to hunting pressure along the coast (Williams, pers. obs.). The current population size is difficult to estimate, but *P. albipennis* probably numbers fewer than 100 birds (John P. O'Neill and Enrique Ortiz, pers. comm.).

TAXONOMIC HISTORY

The first taxonomic treatments of *P. albipennis* (Ogilvie-Grant 1896, Peters 1934) considered the species allied to *P. ortoni* of the west slope of the Andes of Colombia and Ecuador. Peters (1934) and Vuilleumier

(1965) speculated that *P. albipennis* represented a partial albino of *P. ortoni*, despite the fact that Stolzmann (*in* Ogilvie-Grant 1896) reported seeing other birds with white wings. Hellmayr and Conover (1942) pointed out that *P. albipennis* is much larger than *P. ortoni* and questioned their close relationship. Vaurie (1966a:10, 1968), who reviewed the taxonomic history in detail, pointed out that Stolzmann was a "reliable and painstaking" observer and stated that his accounts of seeing other white-winged birds were probably accurate. This evidence combined with size and plumage differences between *P. albipennis* and *P. ortoni* led Vaurie (1968) to conclude that *P. albipennis* was a distinct species, but he did not speculate on its taxonomic affinities. Delacour and Amadon (1973) also discounted the hypothesis of Peters and Vuilleumier and stated that although the affinities of the White-winged Guan were unknown, it was probably related to *P. purpurascens* or *P. jacquacu*.

REVIEW OF RELATED FORMS

The following is a review of the species thought to be most closely related to *P. albipennis*. A map of their distributions is given in Fig. 1.

P. purpurascens (Crested Guan).—This species ranges from Tamaulipas in eastern Mexico and southern Sinaloa in western Mexico south through Central America, and in South America west of the Andes to the cordilleras north of Zaruma, Ecuador, and in the Magdalena Valley of Colombia to the headwaters of the Río Magdalena. Crested Guans also occur eastward across Venezuela, north of the Orinoco to its delta (Delacour and Amadon 1973). There is clinal geographic variation from north to south. The amount of rufous in the plumage increases, while the amount of white edging of feathers of the mantle and overall size decrease. Nonetheless, three subspecies are recognized (Delacour and Amadon 1973).

P. purpurascens is primarily a bird of lowland and lower montane rain forest, but is not restricted to dense forests. Throughout its range *P. purpurascens* also frequents subtropical forests up to 2700 m and occurs in the drier areas of western Mexico and Central America (Slud 1964, Dickey and van Rossem 1938).

P. jacquacu (Spix's Guan).—This species ranges from Guyana through Venezuela south of the Orinoco, in western Brazil east to the upper Tapajos and Rio Xingu, south to Para and northern Mato Grosso. It is also found in the eastern parts of Colombia, Ecuador, and Peru and into northern Bolivia (Delacour and Amadon 1973). Spix's Guan is found most often in tropical forests, locally up to 1360 m (AMNH 115876, Peru, Dpto. San Martin). Several Ecuadorian specimens examined had the notation "subtropical zone." The four subspecies recognized by Delacour and Amadon (1973) differ slightly in size, plumage hue, amount of white on certain
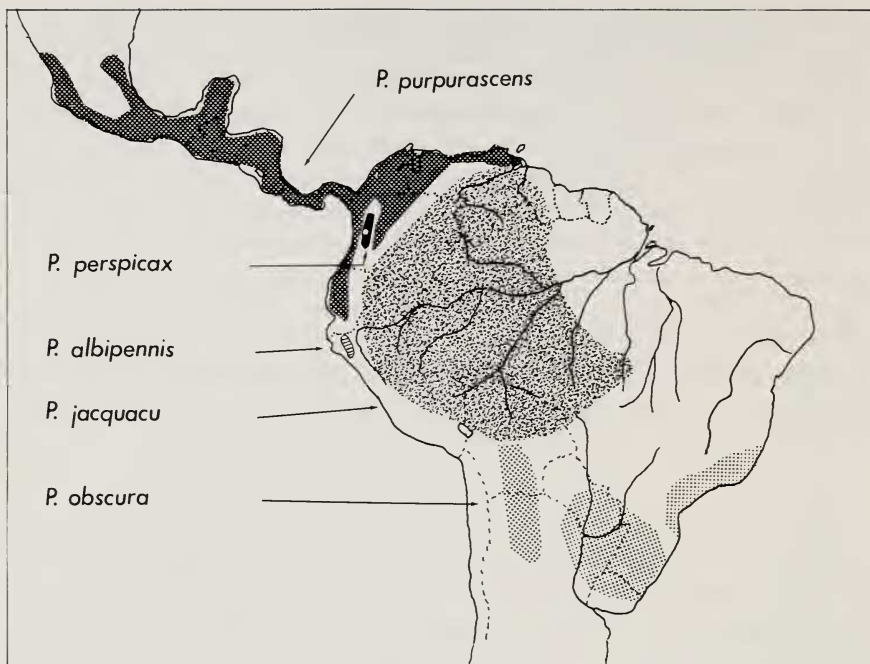
FIG. 1.   Ranges of five closely related species of *Penelope* (from Vaurie 1968).

feathers, and shape of the crest. There is considerable intergradation between the races.

P. perspicax (Cauca Guan).—This guan is restricted to the subtropical slopes of the western Andes and eastern slopes of the central Andes in the Cauca Valley of Colombia (Delacour and Amadon 1973). There is controversy over the taxonomic status of the Cauca Guan. Vaurie (1966a) considered it a subspecies of *P. jacquacu*, citing similarities in the white edgings of certain shoulder feathers and the wing-tail ratio. Delacour and Amadon (1973) treated it as a full species and stated that its relationships lie with *P. purpurascens*, mainly because both lack a tracheal loop. Hellmayr and Conover (1942) considered the plumage differences to be of subspecific importance only, and listed *P. perspicax* as a zonal representative of *P. purpurascens*.

P. obscura (Dusky-legged Guan).—*P. obscura* occurs in three disjunct populations: one in eastern Brazil from Espirito Santo, Río de Janeiro, and southeastern Minas Gerais south through São Paulo and Parano to Santa Catarina; the second from southeastern Brazil in Río Grande do Sul west to northeastern Argentina, Paraguay and Uruguay; and the third from

central Bolivia south to northwestern Argentina (Vaurie 1968). The three subspecies recognized by Delacour and Amadon (1973) differ in coloration, size, and amount of white on the crest feathers. No intergradation between races has been demonstrated. Vaurie (1968) believed the distributional gap between the two western races to be a secondary modification of the range caused by an increase in aridity of the Chaco, which isolated the ancestral form into two allopatric populations.

The Dusky-legged Guan is found in tropical zone forest and also in montane areas up to 2000 m (ANSP 162364, Bolivia, Dpto. Chuquisaca) where lower elevations are too dry for evergreen forest (Delacour and Amadon 1973). The Bolivian race (*bridgesi*) is most often found at higher elevations, especially where its range approaches that of *P. jacquacu*.

TAXONOMIC CHARACTERS

Previous workers have not agreed on which taxonomic characters should be used to distinguish the Cracidae at the species level. The family is diverse in plumage, internal morphology, behavior and vocalizations, but the genera are delimited by conspicuous sets of characters. Most species of *Crax* (including *Mitu*), for example, possess a casque, frontal protuberance, or some modification of the bill. All members of *Penelope* have a wattle, dewlap, or areas of naked skin on the throat, and species of *Ortalis* exhibit uniformity in plumage pattern, voice, tracheal structure and tendency to polygamy (Vuilleumier 1965).

Within *Penelope* researchers have used a variety of characters to define species limits. Peters (1934) and Hellmayr and Conover (1942) considered various features of external morphology (absolute measurements and plumage pattern) sufficient to delineate closely related species. Vuilleumier (1965) stated that due to the overall clinal variation in the *P. purpurascens-jacquacu-obscura* group, no more than a single species should be recognized. Vaurie (1968) used body proportion, shape of the crest, tarsus color, or a combination of these characters in his analysis. Blake (1955) made the observation that there was no one character that separated *P. purpurascens* from *P. jacquacu*, and concluded that the two were conspecific, a view he no longer holds (Blake 1977). Blake did not suggest merging *P. obscura* with this group, as did Vuilleumier (1965), because he considered the black tarsus and different body proportions of *P. obscura* important specific characters. Delacour and Amadon (1973) believed that the wing-tail proportions used by Vaurie as a specific character were unimportant, and stated that the fact that *P. jacquacu* had a tracheal loop and *P. purpurascens* did not should be weighed heavily. The value of this taxonomic character is not clear and its possible significance is discussed in the following section.

The tracheal loop in the Cracidae.—The family Cracidae shows an unusual amount of variation in the modification of the trachea (Delacour and Amadon 1973). The function of a lengthened trachea is twofold: to impede higher frequencies (thus lowering the pitch of the call), and to increase volume (Clench 1978). In all chachalacas (*Ortalis*) a loop is present in males, but not in females, and this is associated with the loud, raucous calls characteristic of the group. Curassows show some variation between and within genera. *Nothocrax*, noted for its booming song, has a long tracheal loop, as does the Helmeted Curassow (*Pauxi pauxi*, sometimes considered *Crax*), which has a low, droning call (Delacour and Amadon 1973). Members of the *Crax rubra* (Great Curassow) superspecies have a tracheal loop, but in a reduced form. There is a peculiar flattening in the trachea of these species which may serve the same function as a long loop.

The situation in guans is more complex. In *Penelope*, six species have a loop, but four species do not. When present, there is some variation in its degree of modification. In the more aberrant guans (*Aburria*, *Chamaepetes*, *Penelopina* and *Pipile*), there is no tracheal loop. Delacour and Amadon (1973) speculated that the absence of a loop might be related to the whistled song of those groups, and that perhaps the trend in guans is toward the loss of the modified trachea and the "crowing" calls associated with it. The unusual Horned Guan (*Oreophasis derbianus*) also lacks a tracheal loop, although it has a low "mooing" call, reminiscent of the booming of the curassows. Vuilleumier (1965) considered the aberrant guans to be closer to the ancestral form. He stated that they have conserved some of the "primitive" characters such as very arboreal habits, ecological association with humid forests, and lack of patterned plumage. This might lead one to speculate that lack of a tracheal loop is also a primitive condition, but the evidence seems too meager to support such a conclusion.

Although the tracheal loop is a variable character among the species of *Penelope*, its presence or absence seems consistent within a species. Tracheal loops are used to modify voice, which is likely to be an important isolating mechanism in cracids. It is probable that voice, presence or absence of a loop, and wing-whirring displays form an important suite of characters for classifying this group at the species level.

SIZE DIFFERENCES IN *PENELOPE* AND THE PROBLEM OF *P. ORTONI*

Peters (1934) and Vuilleumier (1965) considered *P. albipennis* (a large species) to be closely related to *P. ortoni* (a small species) of the Pacific lowlands of Colombia and Ecuador south to Guayaquil. Vuilleumier (1965) noted that six birds collected from one population of *P. ortoni* in Colombia had some white areas scattered throughout the plumage, and he considered *P. albipennis* to be a similar partial albino. It is now known that

presence of white wings in *P. albipennis* is the normal condition. The partial albino hypothesis can be discounted. Nevertheless, the possibility that *P. albipennis* is closely related to *P. ortoni* must be considered.

Vaurie (1966b) stated that differences between *P. albipennis* and *P. ortoni* in size and in coloration of the crest indicate that the two species are probably not closely related. The mean wing and tail length obtained for *P. ortoni* males by Vaurie (1968) was 269.3 ± 8.5 mm and 235.8 ± 11.3 mm, respectively (24 specimens measured). For males of *P. albipennis* both wing and tail average 337 mm. No two species of *Penelope* considered closely related show size differences of this magnitude. Vaurie (1968) also stated that *P. ortoni* does not vary geographically. Since size seems to be an important character in delineating relationships at the species level in *Penelope*, it seems unlikely that an isolated population of *P. ortoni* could become one-third larger than "normal" *P. ortoni*.

Chapman (1917, 1926) lists *P. ortoni* as a representative species of the Colombian-Pacific fauna of western Colombia and Ecuador, and points out this avifauna is strikingly unlike the equatorial-arid fauna found farther south. He states also that this Colombian-Pacific avifauna was derived from Amazonia before the final uplift of the Andes, and that its isolation and differentiation was due to Pleistocene orographic events. Haffer (1967) agreed that most of the birdlife of the Colombian-Pacific fauna was derived from Amazonia but he suggested that it had crossed the northern end of the Andes at the beginning of the Pleistocene before the final uplift of the Andes. He stated that the isolation of this fauna was due to repeated wet-dry climatic cycles during the Pleistocene that created forest refugia in western Colombia.

The above evidence and speculation lead me to suggest that *P. ortoni* was derived from an ancestral stock that moved into western Colombia from Amazonia during the Pleistocene. Its nearest living relative appears to be *P. marail* of southern Venezuela and northern Brazil. The two species are similar in size (in males of *P. marail* the wing averages 281 mm and the tail 253 mm), and both share a dull, unpatterned plumage. It seems likely that the ancestral proto-*P. marail-ortoni* form had a wide distribution over much of tropical South America during the Pleistocene, and that climatic fluctuations, according to the model proposed by Haffer (1967), enhanced the formation of at least three species: *P. ortoni*, *P. marail*, and *P. superciliaris* a similar-sized species found south of the Amazon in Brazil, Paraguay and northeastern Argentina.

SPECIATION MODELS FOR *P. ALBIPENNIS*

The avifauna of southwestern Ecuador and northwestern Peru displays a 35% level of endemism (58 of 166 species are endemic), more than the

Santa Marta Mountains of Colombia (9.9%) and the Pantepui of Venezuela (30.2%) (Vuilleumier 1975). In his study of this avifauna, Chapman (1926) concluded that almost half (23 of 57 in his analysis) of the endemic species were derived from forms from the interior of South America. Only eight were thought to have been derived from Central American forms; the remaining 26 were of uncertain affinities. *P. albipennis*, the most differentiated of the large species of *Penelope*, should be included in Chapman's equatorial-arid fauna. At the time of Chapman's work in the 1920's, *P. albipennis* was thought to be extinct or nearly extinct and was not included in his analysis.

The two latest treatments of the Cracidae (Vaurie 1968, Delacour and Amadon 1973) have implied that *P. albipennis* was derived from *P. purpurascens* or *P. jacquacu*. These authors did not speculate on how this derivation of *P. albipennis* might have occurred. Haffer (1974) has offered explanations for the mechanisms of species formation during the Pleistocene and for many of the distribution patterns observed in birds in South America today. The following are three models proposed by Haffer for other species groups that may be relevant to the origin and speciation of *P. albipennis*. (1) Early in the Pleistocene, a widespread, undifferentiated proto-*P. purpurascens-jacquacu* ancestral population was divided by the rising Andes and subsequent climatic changes into five forms which today are the species *P. purpurascens*, *P. jacquacu*, *P. perspicax*, *P. albipennis* and *P. obscura*. *P. albipennis* would not be more closely related to *P. purpurascens* or *P. jacquacu*, but to the common ancestor of both. (2) *P. purpurascens* and *P. jacquacu* were once a widespread, undifferentiated single species that had a continuous distribution over Central and South America (extending into northern Peru). This ancestral form was separated early in the Pleistocene by climatic changes (Haffer 1974) and the rising Andes, which resulted in two incipient species (proto-*P. purpurascens* and proto-*P. jacquacu*). Later in the Pleistocene, a proto-*P. albipennis* was probably isolated from the proto-*P. purpurascens* stock in northwestern Peru. (3) In the late Pliocene or early Pleistocene, *P. purpurascens* and *P. jacquacu* were a widespread, undifferentiated single species. Climatic changes in the Pleistocene and the rising Andes separated the proto-*P. purpurascens* stock in northwestern South America. As the Andes reached their present height, the proto-*P. albipennis* was isolated in northwestern Peru from a westward extension of the proto-*P. jacquacu* stock. The southern limit of proto-*P. purpurascens* at this time was probably not as close to proto-*P. albipennis* as it is today.

Thus in model 1, *P. albipennis* is not any more closely related to *P. purpurascens* than to *P. jacquacu*; in model 2, *P. albipennis* is more closely related to *P. purpurascens* than to *P. jacquacu*; and in model 3, *P. albipennis* is more closely related to *P. jacquacu* than to *P. purpurascens*.

ANALYSIS OF MORPHOMETRIC DATA

Two recent taxonomic treatments of *Penelope* (Vaurie 1968, Delacour and Amadon 1973) have been based upon some aspect of morphometrics in addition to overall plumage pattern. Usually this consisted only of delimiting certain measurements, such as range and mean length of wing, tail, tarsus and exposed culmen, and then making taxonomic conclusions based on qualitative evaluation of these data. For example, Vaurie (1968) calculated the mean, range and standard deviation of wing, tail, tarsus and bill length of all species of cracids and used these descriptive statistics to support his phylogeny for the family.

Prior to the present study, a simultaneous assessment of a number of characters has not been attempted for the Cracidae. Multivariate analysis of six characters used in this study show how *P. purpurascens*, *P. jacquacu* and *P. obscura* fall into natural groupings according to mensural data, and why these natural groups might reflect phylogeny.

METHODS

The statistical analysis was based on measurements from specimens of *Penelope* from the Louisiana State University Museum of Zoology (LSUMZ), the American Museum of Natural History (AMNH), the Academy of Natural Sciences of Philadelphia and the U.S. National Museum (USNM). Six measurements were taken from each specimen: wing chord, length of tail, length of tarsus, length of culmen from anterior portion of the nostril, height of culmen at anterior edge of the nostril, and width of culmen at anterior edge of the nostril. If a specimen showed excessive wear in any of these characters, that character was not measured on that specimen. *P. albipennis* and *P. perspicax* were not included in the analysis due to inadequate sample size. Only those specimens of *P. purpurascens*, *P. jacquacu* and *P. obscura* from which all six measurements were taken could be used in the analysis.

These mensural data were analyzed using a multivariate analysis of variance (MANOVA) (Kendall and Stuart 1961) for the six characters for each sex to test for significant differences between species (overall species effect). Since the northern subspecies of *P. purpurascens* is noticeably larger than the southern, and since *P. albipennis*, if derived from *P. purpurascens*, would almost certainly be closely related to the southern one, the MANOVA was run twice, eliminating the specimens of the northern subspecies from the second analysis.

A discriminant analysis (Sneath and Sokal 1973) was used on the six characters for each sex to obtain pairwise squared generalized distances between *P. purpurascens*, *P. jacquacu* and *P. obscura* (Mahalanobis distance). Again, I used only specimens for which all six measurements were available. Nine specimens of *P. perspicax* were classified in the analysis as one of the three species used in the discriminant analysis to determine which species of *Penelope* it most closely resembled morphologically (posterior probability of membership) (Kendall and Stuart 1961).

RESULTS

The MANOVA comparison, using Wilk's Lambda criterion (Timm 1975) of *P. purpurascens*, *P. jacquacu* and *P. obscura* (including all subspecies of *P. purpurascens*) to test for no overall species effect showed that all three species were highly significantly different ($P \leq 0.01$) in the six char-

TABLE 1
MAHALANOBIS DISTANCES FOR THREE SPECIES OF *PENELOPE*

Males	Generalized squared distance to		
From	*P. jacquacu*	*P. obscura*	*P. purpurascens*
P. jacquacu	—	14.84	31.78
P. obscura	13.22	—	28.53
P. purpurascens	28.19	43.19	—

Females	Generalized squared distance to		
From	*P. jacquacu*	*P. obscura*	*P. purpurascens*
P. jacquacu	—	28.16	34.58
P. obscura	12.17	—	36.59
P. purpurascens	26.77	104.58	—

acters using either sex. Since eliminating the larger, northern subspecies of *P. purpurascens* did not affect the results of the tests, all subsequent data given include all subspecies of *P. purpurascens*.

The generalized squared distances between species are given in Table 1. In the procedure used, the Mahalanobis distance between groups (in this case, the species) is measured from the outer edge of one group hyperspace to the innermost point of another group hyperspace. Because the univariate character variation of the three species used here is not the same, the distances between any two hyperspaces are not "symmetrical," i.e., the distance between *P. jacquacu* to *P. obscura* is not the same as that between *P. obscura* and *P. jacquacu*. Nevertheless, it is clear that the *P. obscura* is consistently closer to *P. jacquacu* than to *P. purpurascens*. A classification summary posterior probability of membership (Kendall and Stuart 1961) into each species is given in Table 2. The high percentages of specimens correctly classified indicate that there is little overlap among the species in the six-dimensional space. Of nine specimens of *P. perspicax* identified as one of three taxa used in the discriminant functions analysis, eight were classified as *P. jacquacu* and one as *P. obscura*. This indicates that *P. perspicax* is morphometrically more similar to *P. jacquacu* than to either *P. obscura* or *P. purpurascens*.

Results of the previous analysis indicate that the four species of *Penelope* examined differ significantly in size. Mayr (1969) cautioned that significant size differences in species could bias the results of analysis of mensural data. Since the species considered in this analysis are of roughly the same size, there is considerable overlap in the mensural data, which

TABLE 2
POSTERIOR PROBABILITY OF MEMBERSHIP AND PERCENT CLASSIFIED INTO EACH SPECIES FOR THREE SPECIES OF *PENELOPE*

Males From	No. of observations and percents classified into:			Total
	P. jacquacu	*P. obscura*	*P. purpurascens*	
P. jacquacu	34	1	1	36
	94.44	2.78	2.78	100.00
P. obscura	0	10	0	10
	0.00	100.00	0.00	100.00
P. purpurascens	1	0	36	37
	2.70	0.00	97.30	100.00

Females From	No. of observations and percents classified into:			Total
	P. jacquacu	*P. obscura*	*P. purpurascens*	
P. jacquacu	23	2	0	25
	92.00	8.00	0.00	100.00
P. obscura	0	9	0	9
	0.00	100.00	0.00	100.00
P. purpurascens	0	0	25	25
	0.00	0.00	100.00	100.00

statistically minimizes the size-related bias. When the results of the previous statistical analysis are examined, certain trends between the species are apparent. *P. purpurascens* and *P. jacquacu* are distinct. *P. obscura* is also distinct, but much more similar to *P. jacquacu* than to *P. purpurascens*. *P. perspicax* is also very similar to *P. jacquacu*, as evidenced by the high probability of its classification as *P. jacquacu* in eight of nine specimens. Tables 3 and 4 show that *P. jacquacu*, *P. obscura*, and *P. perspicax* also share a wing-tail ratio of less than 1.

ANALYSIS OF VOCALIZATIONS

Vocalizations of birds of the genus *Penelope* are poorly documented. The recorded species are known to be highly vocal and to possess a wide variety of call and alarm notes. Most species of *Penelope* have three basic vocalizations: a loud alarm "scream"; a soft *whit whit* given either to maintain contact with conspecifics or as a mild alarm call given in the presence of an intruder; and a species-specific "yelping" call used in delineating territories (Paul Schwartz, in litt.). The following is a comparison of the various calls of *P. purpurascens*, *P. jacquacu* (recorded by P.

TABLE 3

MEAN, SE, AND RANGE FOR SIX CHARACTERS OF MALES OF FIVE SPECIES OF *PENELOPE*

Characters	N	P. jacquacu	N	P. obscura	N	P. albipennis	N	P. perspicax	N	P. purpurascens
Bill length	53	16.48 ± 0.152 (13.45–18.56)	13	15.83 ± 0.267 (14.57–17.81)	0	—	4	17.48 ± 0.158 (17.07–17.73)	64	17.59 ± 0.155 (14.59–20.04)
Bill width	61	8.42 ± 0.072 (7.25–9.73)	13	8.70 ± 0.23 (7.30–9.76)	0	—	4	8.92 ± 0.226 (8.30–9.36)	71	9.16 ± 0.070 (7.22–9.99)
Bill height	63	7.70 ± 0.070 (6.21–9.04)	13	8.17 ± 0.19 (6.73–9.30)	0	—	4	7.64 ± 0.09 (7.43–7.84)	71	7.98 ± 0.073 (6.17–9.50)
Tail length	46	331.83 ± 2.594 (300.00–369.00)	10	326.80 ± 8.546 (289.00–370.00)	1	325.00	4	333.75 ± 6.524 (315.00–345.00)	43	369.37 ± 4.479 (328.00–446.00)
Wing length	63	315.90 ± 1.993 (282.00–353.00)	12	317.67 ± 9.447 (253.00–356.00)	1	336.00	4	315.00 ± 4.243 (307.00–325.00)	70	379.60 ± 2.223 (341.00–419.00)
Tarsus length	63	82.45 ± 0.477 (69.35–93.60)	12	81.23 ± 1.459 (73.30–90.90)	1	90.00	4	80.95 ± 1.584 (76.63–84.23)	68	85.21 ± 0.445 (75.85–95.52)
Wing-tail ratio		0.95		0.97		1.03		0.94		1.03

TABLE 4

MEAN, SE, AND RANGE FOR SIX CHARACTERS OF FEMALES OF FIVE SPECIES OF *PENELOPE*

| Characters	N	*P. jacquacu*	N	*P. obscura*	N	*P. albipennis*	N	*P. perspicax*	N	*P. purpurascens*
Bill length	33	15.29 ± 0.280 (11.05–19.1)	12	15.33 ± 0.456 (12.60–17.96)	1	16.15	5	15.54 ± 0.483 (13.80–16.40)	49	17.01 ± 0.266 (7.50–19.50)
Bill width	36	8.11 ± 0.100 (6.75–9.34)	12	8.09 ± 0.284 (6.75–9.99)	1	9.36	5	8.23 ± 0.131 (7.85–8.62)	54	9.00 ± 0.083 (7.80–9.90)
Bill height	36	7.02 ± 0.103 (5.87–8.65)	12	7.50 ± 0.232 (6.05–8.79)	1	7.40	5	7.42 ± 0.158 (6.80–7.69)	55	7.72 ± 0.085 (6.45–9.60)
Tail length	30	319.03 ± 3.263 (290.00–374.00)	9	319.33 ± 7.599 (289.00–345.00)	2	342.50 ± 17.50 (325.00–360.00)	5	326.60 ± 5.784 (310.00–340.00)	33	367.64 ± 5.311 (316.00–424.00)
Wing length	38	300.21 ± 2.820 (260.00–347.00)	11	308.09 ± 7.288 (282.00–351.00)	2	337.00 ± 12.00 (325.00–349.00)	5	305.40 ± 3.669 (293.00–315.00)	56	370.30 ± 2.718 (327.00–410.00)
Tarsus length	37	79.30 ± 0.524 (72.90–86.01)	12	78.51 ± 1.429 (69.55–87.15)	2	79.50 ± 1.50 (78.00–81.00)	5	77.59 ± 1.053 (74.88–80.15)	52	83.85 ± 0.562 (76.14–94.72)
Wing-tail ratio		0.94		0.97		0.98		0.94		1.01
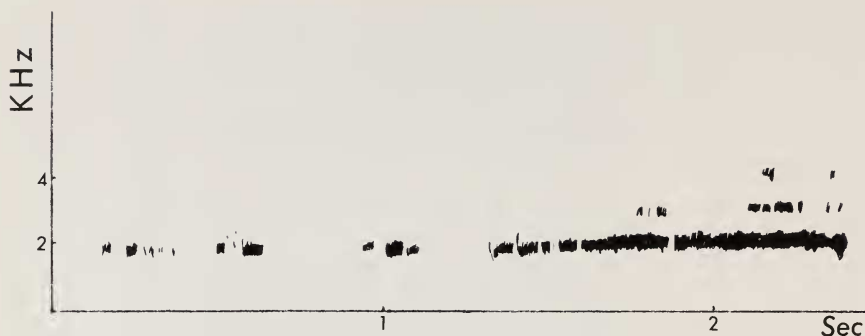
Fig. 2.   Sonograms of "trumpeting" call of *P. jacquacu.*

Schwartz) and *P. albipennis* (recorded by T. Parker), and a discussion concerning the possible taxonomic significance of the similarities and differences. The sonograms presented in this study were prepared using a Voice Identification System Analyzer Model No. 700. Tracings were made of the original sonograms to eliminate excess background noise.

The "yelping" call, or a variation thereof, is found in all three species. In *P. jacquacu*, "yelping" is replaced by a call consisting of loud "trumpeting," which is often preceded by a series of low, introductory notes (Fig. 2). Occasionally, "trumpeting" is uttered softly, and it resembles the "yelp" of *P. purpurascens* and *P. albipennis*. "Trumpeting" of *P. jacquacu* seems to have the same function as the "yelping" call of *P. purpurascens* and *P. albipennis*, and is probably associated with the presence of a tracheal loop (P. Schwartz, in litt.). The "yelping" calls of *P. purpurascens* and *P. albipennis* are similar (Fig. 3). In both species, the call is softer than "trumpeting" of *P. jacquacu*, and usually has a faster cadence. It is noteworthy that neither species has a tracheal loop (Delacour and Amadon 1973; Gustavo del Solar, in litt.). These rapid calls are often preceded by a low growling that rises in pitch to become the plaintive "yelp."

An additional call shared by the three species is a short, low-pitched *whit*, given repetitively. The call is basically the same among the three species, and is probably used either to indicate mild disturbance or to maintain contact with conspecifics (Delacour and Amadon 1973).

Other studies have shown that similar vocalizations in groups of birds are reliable indicators of relationship (Johnson 1963, Lanyon 1978). The "yelping" calls of *P. purpurascens* and *P. albipennis* are much more similar to each other than either is to "trumpeting" of *P. jacquacu*. This suggests a close phylogenetic relationship between *P. purpurascens* and *P. albipennis*. The reasons for modification of this call in *P. jacquacu*,
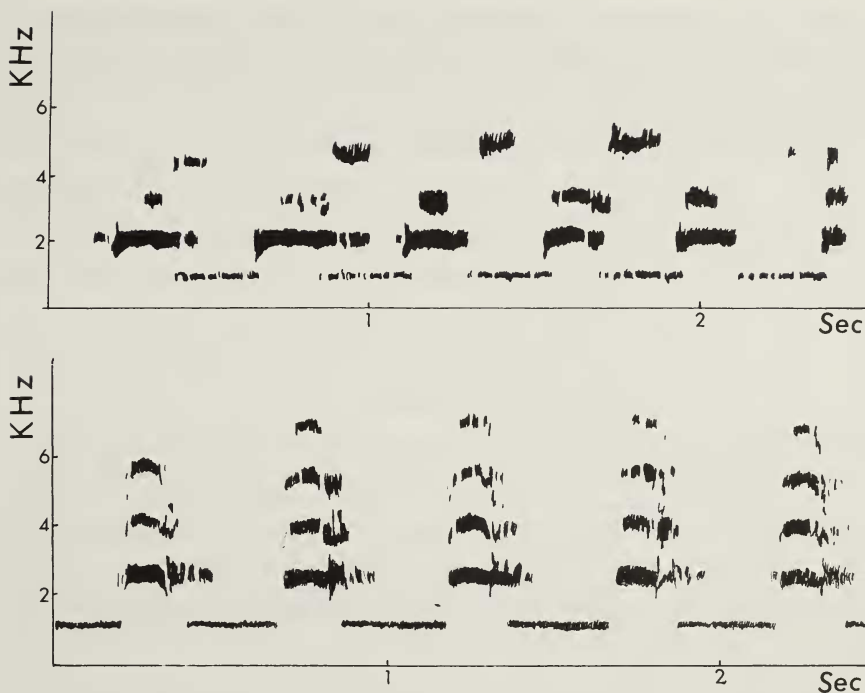
FIG. 3.   Sonogram of "yelping" calls of *P. purpurascens* (above) and *P. albipennis* (below).

and its associated changes in tracheal structure, are not apparent. A possible explanation could be that in many parts of the Amazon Basin there are up to five (or possibly six) species of sympatric cracids (Delacour and Amadon 1973). The presence of several related sympatric species could have selected for increased vocal divergence through development of a tracheal loop. It is known that the loud, crane (*Grus*)-like "yelp" of *P. jacquacu* is completely unlike the calls of any other cracid in South America. An alternative explanation would be the possibility that all *Penelope* once had a tracheal loop, now lost in those forms inhabiting areas where fewer cracids are found.

DISCUSSION

My data show that certain morphological, distributional and behavioral trends are apparent within several species of *Penelope*. *P. purpurascens* and *P. albipennis* are vocally more similar to each other than either is to the other species found east of the Andes, namely *P. jacquacu* and *P. obscura*, both of which have a tracheal loop and are morphometrically

similar in six characters. *P. perspicax* is said to lack a loop (a living specimen examined by C. Lehmann, *in* Delacour and Amadon 1973), but it appears to be much closer to *P. jacquacu* in morphometrics and overall plumage coloration.

P. albipennis and *P. purpurascens* possess more unique characters than *P. jacquacu* and *P. obscura*. The bushy crest and large size of *P. purpurascens* set it apart from the other species and prompted Vaurie (1968:192) to state that *P. purpurascens* is "the most aberrant member of this complex" (*P. jacquacu*, *P. purpurascens*, and *P. obscura*). Vaurie did not include *P. albipennis* in his analysis because the species was known from only three specimens at the time of his study. *P. albipennis* possesses three unique characters: white primaries, a bicolored bill (blue, with a black tip), and a dark, greenish-gray plumage. The facial skin is also rosy slate in color instead of the bluish slate found in the other large *Penelope*.

With the above evidence one may evaluate the speciation models presented earlier in this paper. In model 1, all the species of *Penelope* are equally related and so the species would not exhibit the morphological and vocal trends shown by the data in this study. If model 3 was correct, *P. albipennis* and *P. jacquacu* should appear similar in vocalizations, and both should be different from *P. purpurascens*. This model is also not supported by the data.

The simplest explanation for the speciation of *P. albipennis* seemingly would be that encompassed by model 2. Proto-*P. purpurascens* and proto-*P. jacquacu* were separated early in the Pleistocene (or late in the Pliocene) and evolved the morphometric and vocal differences apparent between the two modern species. Later in the Pleistocene, proto-*P. albipennis* became isolated from the proto-*P. purpurascens* stock in northwestern Peru during one of the alternating wet-dry climatic cycles of western South America documented by Campbell (1979). Isolation in a new habitat type and subsequent contact with *P. purpurascens* during these climatic cycles possibly favored the development of white primaries in *P. albipennis* as a display character. Since the wing-whirring displays of *Penelope* occur above the tree tops in the twilight just before dawn, the increased visibility of white primaries in an open habitat would presumably be selectively advantageous.

The speciation of *P. perspicax* presents an interesting problem. The crest feathers of *P. perspicax* are intermediate between those of *P. purpurascens* and *P. jacquacu* (Delacour and Amadon 1973). Although *P. perspicax* is similar to *P. purpurascens* in some plumage characteristics (Delacour and Amadon 1973), it resembles *P. jacquacu* in others (Vaurie 1968). *P. perspicax* is similar to *P. purpurascens* in lacking a tracheal loop, but

is morphometrically closer to *P. jacquacu*. The confusing mosaic of characters of *P. perspicax* strongly suggests that it has diverged less from the putative common ancestral form than have *P. jacquacu* and *P. purpurascens*. *P. perspicax* may have arisen from the isolation of a population of the ancestral form in the Cauca Valley before the differentiation of *P. purpurascens* and *P. jacquacu*.

P. obscura and *P. jacquacu* are clearly more closely related to each other than to the other species of *Penelope* in plumage, morphometrics and tracheal loop morphology. *P. obscura* was probably isolated from the proto-*P. jacquacu* stock in the Pleistocene in one of the forest refuges of eastern Brazil (see Haffer 1974).

SUMMARY

Lowland guans of the genus *Penelope* (*purpurascens* group) in South America were studied to determine relationships within the group and present a speciation model for its members. New data available for the White-winged Guan (*P. albipennis*) provide insight into its phylogeny and speciation. A multivariate analysis of variance on six characters of *P. purpurascens*, *P. jacquacu*, *P. perspicax*, and *P. obscura* indicates that *P. jacquacu* and *P. purpurascens* are significantly different from each other in six characters, and that *P. perspicax* and *P. obscura* are more similar to *P. jacquacu* than to *P. purpurascens*. Analysis of vocalizations shows that *P. albipennis* calls are more similar to those of *P. purpurascens* than to those of *P. jacquacu*. Three speciation models proposed for *Penelope* were evaluated in light of the above data. The selected model proposed that *P. albipennis* was isolated in western Peru after the differentiation of a proto-*P. purpurascens* from proto-*P. jacquacu*. *P. perspicax* shared characters with both *P. purpurascens* and *P. jacquacu*, and was postulated to be closer to the ancestral form. *P. obscura* was clearly more closely related to *P. jacquacu* and was probably isolated in a forest refugium in eastern Brazil.

ACKNOWLEDGMENTS

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MUSEUM OF ZOOLOGY, LOUISIANA STATE UNIV., BATON ROUGE, LOUISIANA 70893. (PRESENT ADDRESS: DEPT. BIOLOGICAL SCIENCES, LOUISIANA STATE UNIV. IN SHREVEPORT, SHREVEPORT, LOUISIANA 71115. AC-CEPTED 15 AUG. 1981.

COLOR PLATE

The color plate Frontispiece of the heads of Spix's Guan (*Penelope jacquacu*), White-winged Guan (*P. albipennis*), and Crested Guan (*P. purpurascens*) has been made possible by an endowment established by George Miksch Sutton. The painting is by J. P. O'Neill.

RESEARCH GRANTS

The Eastern Bird Banding Association and the Western Bird Banding Association are each offering research grants of $250 in aid of research using bird banding techniques or bird banding data. Applicants should submit a resume of his or her banding or orthino-logical background, the project plan, and a budget to the Joint Selection Committee Chair-man: Robert C. Leberman, Powdermill Nature Reserve, Star Route South, Rector, Pennsylvania 15677. No formal application forms are available, and the amount requested should not exceed $250. The deadline for receipt of applications is 15 March 1983.

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